Size-dependent sex allocation in *Solanum lycocarpum* St. Hil. (Solanaceae)

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**Abstract**

Resource allocation to reproduction can change depending on size, as predicted by the size-dependent sex allocation theory. This theory is based on the fact that small individuals will invest in the allocation of sex with lower cost of production, usually male gender. In plants, there are some andromonoecy species, presence of hermaphroditic and male flowers in the same individual. Andromonoecy provides a strategy to optimally allocate resources to male and female function, evolving a reproductive energy-saving strategy. Thus, our objective was to investigate the size-dependent sex allocation in *Solanum lycocarpum* St. Hil. We tested the hypothesis that plants with larger size will invest in the production of hermaphroditic flowers, because higher individuals have greater availability of resources to invest in more complex structures involving greater energy expenditure. The studied species was *S. lycocarpum*, an andromonoecious species. From June 2016 to March 2017 the data were collected in 38 individuals, divided in two groups: the larger plant group (*n*=18; height=3-5 m) and the smaller plant group (*n*=20; height=1-2 m). Our data show that there was effect of plant size on the flower production and the sexual gender allocation. The larger plants showed more flowers and higher production of hermaphroditic flowers. Furthermore, in the flower scale, we observed allometric relationship among the flower’s traits with proportional investments in biomass, anther size and gynoecium size. Our results are in agreement with size-dependent sex allocation theory and andromonoecy hypothesis related to mechanisms for optimal resource allocation to male and female function.

**Keywords:** andromonoecy, biomass allocation, floral attributes, sex allocation, size-dependent gender.

**Resumo**

A alocação de recursos para reprodução pode mudar dependendo do tamanho, conforme previsto pela alocação sexual dependente do tamanho. Essa teoria é baseada no fato de que indivíduos pequenos investirão na alocação sexual com menor custo de produção, geralmente do sexo masculino. Nas plantas, existem algumas espécies andromonoicas, presença de hermafroditas e flores masculinas no mesmo indivíduo. A andromonoecia fornece uma estratégia para alocar recursos de maneira ideal às funções masculina e feminina, desenvolvendo uma estratégia reprodutiva de economia de energia. Assim, nosso objetivo foi investigar a alocação sexual dependente do tamanho em *Solanum lycocarpum* St. Hil. Testamos a hipótese de que plantas de maior tamanho investirão na produção de flores hermafroditas, pois indivíduos mais altos economizariam mais disponibilidade de recursos para investir em estruturas mais complexas que envolvem maior gasto de energia. A espécie estudada foi *S. lycocarpum*, uma espécie andromonoica. De junho de 2016 a março de 2017, os dados foram coletados em 38 indivíduos, divididos em dois grupos: o maior grupo de plantas (*n*=18; altura = 3-5 m) e o menor grupo de plantas (*n*=20; altura = 1-2 m). Nossos dados mostraram que houve efeito do tamanho da planta na produção de flores e na alocação sexual. As plantas maiores apresentaram mais flores e maior produção de flores hermafroditas. Além disso, observamos uma relação alométrica entre as características da flor, com investimentos proporcionais em biomassa, tamanho da antera e tamanho do gineceu. Nossos resultados estão de acordo com a teoria de alocação de sexo dependente do tamanho e a hipótese de andromonoecia relacionada a mecanismos para a alocação ótima de recursos para a função masculina e feminina.

**Palavras-chave:** andromonoecia, alocação de biomassa, atributos florais, alocação sexual, sexo dependente do tamanho.

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1. Introduction

Plants have three essential functions: growth, defense against herbivores and reproduction, and each of these functions needs some resources (Weiner et al., 2009). However, the resources are limited and the essential functions compete for them, which generate a trade-off between the essential functions, leading to a resource differential allocation (Bazzaz et al., 1987), as plants are not able to invest simultaneously in growth, reproduction and defense (Weiner et al., 2009). Thus, these differences in resources allocation among different structures or activities are considered a process of partitioning (Weiner et al., 2009).

Sexual allocation is one type of allocation that may occurs in both animals and plants and has as premise that the individual can change his gender taking into account the energy expenditure, opting for the more favorable sex (Warner et al., 1975; Lloyd and Bawa, 1984; Warner, 1988; Vega-Frutis et al., 2014). This modification of the sexual gender will depend mainly on the resources available in the environment (Warner, 1988; Yakimowski and Barrett, 2014). Whether the resource is scarce, the sexual gender will be the one that demands less energy for the individual. In this way, the individual will tend to produce male gametes, which are usually smaller and more numerous in relation to female gametes. This last have a high energy cost to the plant (Warner, 1988). This allocation has been considered a survival strategy because it affects the plant fitness through the male and female functions (Cao and Kudo, 2008).

Another theory that can be linked to the gender change is the size-dependent sex allocation. This theory is based on the fact that small individuals will invest in the allocation of sex with lower cost of production, usually male gender (Lloyd and Bawa, 1984; Vega-Frutis et al., 2014). Larger individuals will have greater availability of maternal resources and will become female. However, the sex allocation can be male-biased in larger plants of wind-pollinated species, such as Ambrosia artemisifolia, and Pennisetum typhoides (Ackerly and Jasieniski, 1990; Dajoz and Sandmeier, 1997). Thus, changes in sexual expression may occur throughout the life of the organism being associated with its increase or decrease in size (Bierzychudek, 1984; Schlessman, 1991; Vega-Frutis et al., 2014; Zhang et al., 2014b). The increase in size is related to the improvements in the post-flowering resources of the plant, which can lead to an increase in female flowers (Lloyd and Bawa, 1984; Klinkhamer et al., 1997). The gender change size-dependent has led to many studies that provide a better understanding of the sexual ratios of flowers and the mechanisms of evolution of the reproductive systems in plants (Cao and Kudo, 2008; Barrett, 2010, 2013; J. Zhang et al., 2014a; Z. Q. Zhang et al., 2014b; Nakahara et al., 2018).

In some angiosperms exist a reproductive system that is called andromonoecy. In this sexual system, the individual has male and hermaphrodite flowers (Vega-Frutis et al., 2014) that can be determinate by expression regulatory genes (Barrett, 2002; Charlesworth, 2002; Diggle et al., 2011; Ming et al., 2011), by epigenetic control (Diggle et al., 2011; Zhang et al., 2014a) or by hormonal influence (Diggle et al., 2011; Zhang et al., 2014a). The hermaphrodite flowers, also called perfect flowers, have both male and female structures and usually they are bigger than male flowers (Diggle et al., 2011; Zhang et al., 2014b). The most studies about maintenance of andromonoecy support the hypothesis that the andromonoecy provides the mechanisms for optimal resource allocation to male and female function (Primack and Lloyd, 1980; Charnov, 1982; Huang, 2003). This hypothesis assumes that because female reproductive success is limited by resources, individual fitness will be enhanced by staminate flowers once female reproductive success is maximized, since the production of staminate flowers should be less costly than perfect flowers (Primack and Lloyd, 1980). According to Lloyd (1980), the sexual strategies to maximizing fitness from reproductive efforts expended during a sexual reproduction episode lead to a better understanding of the evolutionary history of a group. In this way, with this work, we obtained more information about this process and provided important information on aspects of evolutionary biology of the genus Solanum (Solanaceae family). Our goal was to investigate the size-dependent sex allocation in Solanum lycocarpum St. Hil. We also evaluated the allometric relationship among floral parts. This species is andromonoecious; its flowers are pentameric, of lilac color and blooms the whole year, having a peak of flowering in rainy periods (Oliveira-Filho and Oliveira, 1988; Moura et al., 2010; Feliciano and Salimena, 2011). We tested the hypothesis that plants with larger size will produce more flowers than small plants. In addition, large plants will invest more in hermaphrodite flowers than small plants, because higher individuals have greater availability of resources to invest in more complex structures involving greater energy expenditure.

2. Materials and Methods

2.1. Study area

This study was conducted in a pasture area at Universidade Federal de Lavras, within biome Cerrado, in Minas Gerais state. The study area was defined by geographic coordinate 21° 13’47.4”S e 44°57’54.3”W. Lavras climate is classified as Cwb on Köppen climate classification (Dias et al., 2002). The average altitude is around 918m, the annual average precipitation in Lavras region is 1529 mm and the average temperature is 19.5 °C (Dantas et al., 2007; Dias et al., 2002). The soil is poor in essential nutrients, acid, deep and with aluminum toxicity (Furley and Ratter, 1988).

2.2. Studied system

The species Solanum lycocarpum St. Hil. (Solanaceae) is a shrub, characteristic to Brazilian Cerrado and commonly found in roadsides, open lands and pastures. It is known as Wolf’s Plant or Wolf’s Apple, reaching up to five meters high, its crown is rough and thin with fragile branches (Oliveira-Filho and Oliveira, 1988). This plant is resistant, being able to tolerate dry climates, fire and long
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2.4. Data analysis

In order to verify if individuals of the larger plant group produced a higher total of flowers than the individuals of the smaller plant group, as well as if larger plants produce independently more male and hermaphrodite flowers than small plants was applied the Mann-Whitney test.

To analyze whether flower gender influenced floral attributes, anther size and total biomass of flower and if was interaction between the attributes: total biomass of flower versus anther size, diameter of corolla versus anther size, height of the gynoecium versus anther size and height of the gynoecium versus ovary, we used generalized linear mixed model (GLMM).

All analyses were carried out in SYSTAT version 12.

3. Results

The production of flower appeared to be closely linked to plant size, since the number of flowers was significantly greater in plants from the larger group than in plants from lower group (U = 308.000; p < 0.001) (Figure 2).

Larger plants produced 540 flowers, more than twice as many as small plants that produced 213 flowers in total. They produced a greater number of both male flowers (U = 302.500; p < 0.001), and hermaphrodite flowers (U = 254.500; p = 0.018) (Figure 3).

The flower gender did not influence the anther size (F = 0.041, p= 0.52) (Figure 4A) and the total biomass of flower (F = 0.67, p = 0.68) (Figure 4B). However, flowers with a greater diameter of corolla had a greater anther size (F = 33.55, p < 0.001) (Figure 4A).

The anther size increased with the flower biomass (Figure 4B). There was a significant relationship between the total biomass of flower and anther size (r² = 0.22, F = 20.26, p < 0.001). We also found a significant relationship between the gynoecium size and anther size (Figure 5A). Flowers with higher anther had a larger gynoecium (r² = 0.22, F = 7.64, p = 0.01). However, there were no significant relationships between the diameter of corolla and anther size (r² = 0.3, F = 0.81, p = 0.37) (Figure 4A), and between height of the gynoecium and ovary size (r² = 0.025, F = 0.69, p = 0.41) (Figure 5B).

Figure 1. Flowers of Solanum lycocarpum. (A) Hermaphrodite flower; (B) Male flowers. The scale bars units were 3 cm for each picture.
4. Discussion

Our data showed more investments in flower production in larger *Solanum* individuals. They are consistent with Warner (1988) prediction that larger individuals possess more resources and can allocate more of them for reproduction. On the other hand, smaller individuals tend to invest more in vegetative growth (Warner, 1988). Similar result was found by Cao and Worley (2013), in a study carried out with two species of the genus *Cardiocrinum*, which showed that the species that presents larger individuals produces more flowers, once the biomass allocation can be limited by architectural restrictions, and these changes with the plant size (Bartušková et al., 2015). Thus, in this perspective, the allocation for reproductive functions is dependent on canopy size (Müller et al., 2000).

The higher number of flowers has an important ecological and evolutionary role, as this can increases the chances of pollination, fecundation and seed dispersal (Valenta et al., 2017). Conner et al. (1995) showed that the increase in flowers number was determinant to increase the number of pollinator visits. Thus, we can expect that the higher number of flowers in larger individuals can enhance pollinator attraction and facilitate flower handling and pollen deposition (Valenta et al., 2017).

Our data also showed that there was a strong effect of plant size on the flower production and the sexual gender allocation, corroborant our prediction. The larger plants showed a higher production of hermaphrodite flowers, being in the agreement with “size-dependent sex allocation” theory and andromonoecy hypothesis related to mechanisms for optimal resource allocation to male and female function. According to the theory of size-dependent sex allocation, larger individuals have more energy to spend in structures that demand more energy, such as the hermaphrodite flowers (Lloyd and Bawa, 1984; Vega-Frutis et al., 2014). However, the theory of size-dependent sex allocation does not always have a clear pattern for all plant species. For example, *Liliumapertum* (Liliaceae) showed similar result as we found, in which
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between flower genders can be related to the importance of male flowers, as staminate flowers increase pollinator attraction as some staminate flowers are preferred by pollinators or donate more pollen that reaches the stigma than hermaphrodite flowers (Bertin, 1982; Luo et al., 2012; Anderson et al., 2015; Carbonell, 2019). We also observed allometric relationship among the flower’s traits evaluated that indicates the proportional energy investments to build the flowers (Weiner et al., 2009).

Thus, we concluded that the size of S. lycocarpum influences the sexual allocation and this seems to be a plastic response in this species. The andromonoecy also is related with plant size, indicating that larger individuals can have more energy to invest to produce hermaphrodite flowers, in which has an important ecology and evolutionary role.

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References


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